

A Field Study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, W. I.^{1, 2}

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(Text-figures 1-6)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.", William Beebe, *Zoologica*, 1952, 37 (13): 157-184.]

INTRODUCTION

THIS paper is to some extent complementary to a previous paper on the Black and White Manakin, *Manacus manacus* (Snow, 1962). Both species were studied at the same time, largely by the same methods, and in the same locality, an area of primary and secondary forest in the center of the Northern Range of Trinidad.

About 3½ inches long, the Golden-headed is a smaller and lighter bird than the Black and White Manakin. Its bodily proportions are different; its wings are relatively and absolutely longer, and its legs and tail shorter. Correspondingly, its flight is more rapid and agile, and its displays depend more on flight and wing actions

and less on jumping. The male is all black, with a golden-orange cap and red and white thigh feathers; the female is olive-green. The eye is white in the male and the beak pale brown or straw-colored; in the female the eye is variable in color, but darker, and the beak is darker brown. Like other manakins, Golden-headed Manakins feed largely on fruit, which they take on the wing, but insects are also taken. They bathe in streams, and drink from water collected in the leaves of trees.

For a field study, the Golden-headed is less suitable than the Black and White Manakin. Although it is the more abundant species, at least in Trinidad, most of its activities are carried out higher above the ground. It feeds on average higher, it displays up in the trees, at a height of 20 feet or more, and its nests are placed on average much higher above the ground. Also, its very abundance made it difficult to band more than a fraction of the local population. Over 600 individuals were banded in the study area, but when trapping ceased new birds were still being caught far more often than previously-banded birds. Thus much less detailed information was obtained for the Golden-headed than for the Black and White Manakin, especially as regards nesting and the histories of individual birds.

For details of the environment, the reader is referred to the earlier paper. Here it need only be said that the vegetation is transitional between seasonal forest and lower montane rain forest (Beard, 1946); the temperature varies little throughout the year; annual variation in day-length is 74 minutes; the rainfall averages about 100 inches per year; there is a main dry season from January to May, and the wet season lasts for the rest of the year, being usually interrupted

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by a short spell of dry weather in September or October.

Apart from Skutch's study of *P. mentalis* (Skutch, 1949), no detailed study has been made of any species of *Pipra*. A preliminary account of the present work, dealing only with display, has already been published (Snow, 1956). Sick (1959) has described displays of *P. erythrocephala* and *P. fasciicauda*. Niethammer (1956) has briefly described displays of *P. chloromerus*; and Snow has described displays of *P. pipra* and *P. aureola* (Snow, 1961 and in prep.). (I have referred to "displays" and not "the displays" advisedly, as these studies are certainly not complete; I have always found that manakin species, when watched intensively over a long period, reveal a greater repertory of distinct displays than is apparent from more cursory observation). From these studies it is known that the males of some species of *Pipra* display communally, and some solitarily. Of the known species, *P. erythrocephala* is one of those in which communal display is most highly developed.

Since many comparisons with the Black and White Manakin are made in the course of this paper, for brevity I refer to my previous paper simply as "*Manacus*," followed by the relevant page-number in that paper.

As in the previous paper, I am indebted to several persons for help with the field work; especially to my wife, for much help in the mist-netting and in finding nests; to Dr. W. G. Downs and Dr. T. H. G. Aitken, for making available to me the birds trapped in the course of the work of the Trinidad Regional Virus Laboratory; and to Mr. N. Y. Sandwith and Dr. J. J. Wurdack for many plant identifications. The whole work was generously supported by National Science Foundation Grants G 4385 and G 21007.

THE POPULATION

The Golden-headed Manakin is probably the most abundant forest bird in Trinidad. At the main trapping place, on the edge of secondary forest, and at two subsidiary trapping places two and four hundred yards inside the forest, 625 different individuals were caught over a period of $3\frac{1}{4}$ years. When trapping ceased, as already mentioned, more new individuals were still being caught than previously-banded birds. In the last four months of trapping, 89 new birds and 32 previously-banded birds were trapped. Up to that time, 529 individuals had been caught. Allowing an annual mortality of 10% (see later in this section), about 440 of these would have been expected to be still alive. With the proportion of recaptures to total captures at 32/121 or 26%,

the total population from which the captured birds were drawn should have been of the order of 1,700.

This calculation is clearly subject to considerable error, as the ringed and unringed birds were certainly not randomly mixed within the population, and it is not known how far individuals range in the course of their daily activities. Probably most of those caught lived within the steep-sided forested valley, of about 200 acres, formed by the stream along which the trapping places were situated. It may reasonably be supposed that the density of Golden-headed Manakins in this area was certainly more than one per acre, and probably several times as great.

The Black and White Manakin, probably the next commonest species of forest bird in the study area, was found to have an adult density of just over one bird per acre.

The annual mortality of adults can be estimated approximately from the proportion of adult males in the population. Of the first 100 birds caught at the main trapping places (feeding and bathing places away from the display grounds), 45 were adult males. Of the second 100 caught, 44 were adult males. Thereafter the proportion of adult males declined to around 35% and remained at this figure. This decline was probably due to the fact that adult males are more sedentary than females and young birds, being closely attached to their display grounds, and many of those whose display grounds were nearest the trapping places had by then been caught and were tending to avoid the trapping area.

Male Golden-headed Manakins moult into adult plumage at the beginning of their second year of life. A population in which the sex ratio is equal (as it is in *Manacus* and probably is also in the Golden-headed Manakin) and 44% or 45% of the individuals are adult males, should have an annual adult mortality of about 10%, a figure that is very close to that obtained for the Black and White Manakin by another method (*Manacus*, p. 96).

THE DISPLAY GROUNDS

Male Golden-headed Manakins display communally, but in much more diffuse groups than Black and White Manakins. Each male occupies a particular perch, 20 to 40 feet above the ground. The perch selected is usually a more or less horizontal twig under the canopy of a lower story tree, but sometimes a horizontal stretch of vine is used. To be suitable, a display perch must be roughly straight and without side branches, and not too thick (5-10 mm.). It must have a

clear approach from one side at least, to allow the displaying bird to make the display-flight (p. 186).

The males sometimes peck at excrescences on their display perches, and if there are leaves or tendrils of vine hanging near them they habitually pull at them while hovering or hang onto them. As a result the leaves near a display perch are often tattered. Thus Golden-headed Manakins show in some degree the tendency to clear the display area which is so marked in the Black and White Manakins.

The display perches of different males may be several feet apart in the same tree, or several yards apart in neighboring trees. The number of males at a display ground is variable; those that were studied usually had from six to twelve males.

As in *Manacus* (p. 69), display grounds were found to persist year after year in the same places, and the same display perches were used in successive years. Because it is much less obvious that individual perches are in constant use than it is in *Manacus*, there being no equivalent of the court, the persistent nature of the display ground is not apparent to the observer unless he is able to watch an area over a long period. Probably for this reason, Sick (1959) gives the impression that in Brazil the Golden-headed Manakins display randomly in the forest. In Trinidad, random display could indeed be seen at times all over the forest, mainly from juvenile males, but these birds doubtless eventually settled at one of the permanent display grounds.

ELEMENTS OF THE DISPLAY

The Golden-headed Manakin's display movements and postures are highly stereotyped and very diverse. Some are much more often seen than others, and it was not until I had watched the birds for over a year that I saw some of the less common displays. After 5½ years of intermittent observation, with regular weekly watches for the last 13 months of this period, I was confident that I had seen the full range of normal display given by the Trinidad population of the species. As mentioned later (p. 187), there is some evidence that the display differs markedly in the Brazilian population.

As already mentioned, compared with the Black and White Manakin the Golden-headed has relatively long, pointed wings, and short legs. It is extremely agile in flight, and specialized flights are important in its display. It does not hop or jump, but moves sideways or backwards along the perch with very short quick steps that

give the bird the appearance of sliding. In resting posture, it sits hunched, with body-feathers fluffed and legs concealed. When it begins to display its appearance changes markedly; it sleeks its plumage and stretches its legs, so that the red and white thigh feathers appear.

In view of the male's extreme agility in flight, it is of interest that he averages a little lighter and smaller than the female (Appendix). In *Manacus*, in which display depends on specialized wing-feathers and hypertrophy of the muscles of the shoulder region and thighs, the males are heavier than the females and their wings are shorter.

In the following sections, I have for convenience used the same names as Skutch (1949) used, for display movements that are clearly homologous with those of *Pipra mentalis*.

Advertising Calls

Males sitting inactive on their display perches frequently utter advertising calls, which can be arranged in a series of increasing excitement leading up to active display. At lowest intensity they utter an occasional clear "pu." When excitement is a little increased this is followed by a trill and usually a sharp final note: "pu prrrrrr-pt." With mounting excitement the final note is repeated two or three times, the initial "pu" is replaced by one or two sharper notes, and the trill may be lengthened, so that the call becomes "pir pir prrrrrrrr-pt-pt." The first note of the call may be accompanied by an upward flick of the wings. At this stage the bird is likely to break into more active display.

The other calls are characteristically associated with particular display movements, and will be described in the following sections.

Darting Back and Forth

With the legs stretched so that the colored thigh feathers show, and the body held rather horizontally, the bird makes rapid flights to and fro between its main perch and an adjacent perch usually 3-5 feet away. When it has landed it at once turns rapidly about to face the way it came from. In flight between the two perches, the wings make a brisk humming sound audible for about 20 yards. Between bouts of darting back and forth, a very short, sharp "zit, zit" is often uttered.

The About-face

Rapid about-faces, such as are made between darts back and forth, may be repeated while the bird remains perched in the same place. Each turn may be accompanied by an upward flick of the wings.

The Backward-slide

With the legs stretched, the head held low and

the tail elevated, the bird "slides" backwards along its perch for several inches (Text-fig. 1, b and d). The line of the body is usually at an angle of about 45° to the line of the perch, but this varies; sometimes the body is held almost in line with the perch, and occasionally nearly at right angles to it. At the end of the slide the tail is suddenly depressed and fanned, and the wings raised and held vertically above the back (Text-fig. 1, a and e). Half way through the slide, the wings may be suddenly spread horizontally and then closed again (Text-fig. 1, c and f); this movement is often omitted. Very seldom, after sliding one way the bird may turn and slide back in the other direction. This display is silent.

The Display-flight

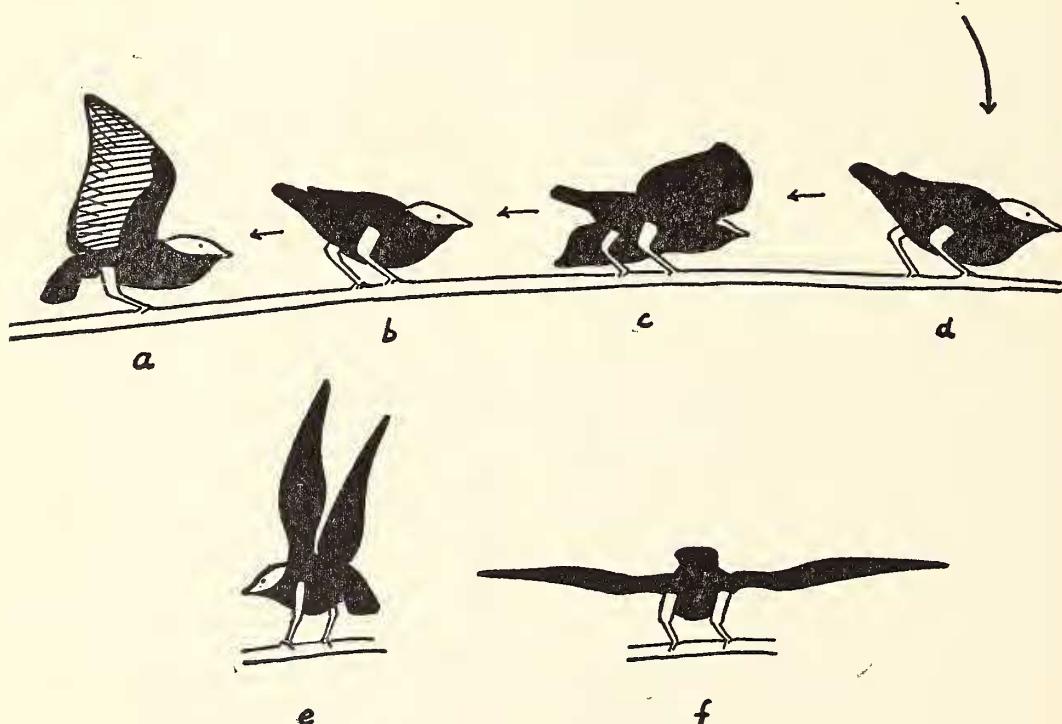
The male leaves his perch and flies with normal flight to a somewhat higher perch about 20-30 yards away. He perches and faces his display perch, utters usually two or three sharp calls, "kew, kew," then takes off and returns to the display perch with extremely rapid flight, uttering a succession of "kew" calls which speed up and become sharper as he nears it. Usually a total of 7-9 "kew" calls are uttered (including those made before taking off). The bird ap-

proaches his display perch with a rapid downward, then upward, then downward swoop, so that its trajectory is a shallow S-curve. As it lands it utters a sharp buzzing call. Thus the listener hears an accelerating series of "kew" calls followed by a sharp buzz, a sequence of sounds that is diagnostic of this display. In this way the display-flights of a group of males can easily be counted even while the observer is watching only one or two of them, as was done during the all-day watch at a display ground described later (p. 190).

Immediately on landing, the bird usually executes a backward-slide. At lesser intensities the slide may not be made, and sometimes the bird lands without uttering the buzzing call. These incomplete displays usually occur if for some reason the bird is put off at the last moment, or apparently misjudges its landing on the perch.

The Frenzied Flutter

This term is used to cover some rather variable movements, having in common that the bird jumps, or makes as if to jump, upwards, and utters an excited "zeek" or "zeek-eek," reminiscent of the buzz made on landing from the display-flight but higher pitched. The bird may



TEXT-FIG. 1. The backward-slide. Arrows show the direction of the bird's movement. b and d: posture while sliding. c and f: wings spread half way through slide. b and e: wings raised and tail fanned at end of slide. a-d shows normal orientation with respect to perch; e and f show less usual orientation transversely to perch. (Drawn from movie film).

jump up or slightly backwards a few inches, with wings conspicuously fluttering, and land back on the same spot; or it may jump up and land a foot or more away with a rapid upward and downward trajectory and a sudden alteration of course in mid-flight; or it may flutter along the perch, moving forwards (not backwards, as when sliding); or it may jump up and flutter, rapidly twizzling from side to side before it lands; or it may simply crouch and flutter its wings violently without leaving the perch. While fluttering it tends to make downward pecking movements which appear to be directed at the perch.

It will be apparent from the foregoing description that this display has much in common with copulation. It is given at times of great excitement and may be thought of as copulation *in vacuo*.

The Upright Posture

When another bird lands on or near a male's display perch, the owner often flies and lands close beside it in a stiff, almost statuesque upright posture (Text-fig. 2). He may not fly straight to the intruding bird, but may make a short circling flight of a few yards away and back, a flight which is sufficiently stereotyped to be regarded as a preliminary part of this display. Just after landing he utters a very sharp, short "zick." The upright posture may be held for several seconds, the bird clinging to the side of the perch rather than perching on it, with the head pointing upwards and the beak often slightly opened. At close quarters it is possible to see that the pupil is greatly contracted while this posture is held. In this display the aggressive element is probably more dominant than in the displays described above. It is often the initial response to an intruder of either sex, and in several cases when it was seen to be made to birds in female plumage there was reason to think that they were young males.

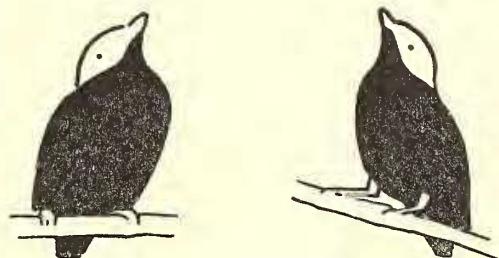
Wing-flicking

General excitement may be shown by quick upward flicks of the wings. Wing-flicks may be interpolated between pivoting, frenzied flutters, and other display movements, or they may sometimes be repeated rapidly by a perched bird and accompanied by the call "pir pir prrrrrr-pt" or the more excited "zeek-eek." Repeated wing-flicking, with calling, appears to constitute an independent display, but one that is less ritualized than those described above.

Sick's Observations in Brazil

Sick's account of the displays of *Pipra erythrocephala* in Brazil (Sick, 1959: 275-277) differs in several respects from that given here. The

Brazilian form (subspecies *rubrocapilla*) is very distinct from the Trinidad form, which is close to the nominate subspecies: the head is red, not golden-yellow, and there is a conspicuous white patch on the under wing-coverts, which is lacking in the Trinidad bird. For the Brazilian bird, Sick does not mention "darting back and forth," the "frenzied flutter" or the "upright posture"; nor does he describe the full "backward-slide" following the "display-flight", which is perhaps the most conspicuous of all the display sequences of the Trinidad birds. He mentions the backward-slide briefly, as being accompanied by quivering of the slightly raised wings, but not the spreading of the wings half way through the slide nor the raising of the wings and fanning of the tail at the end of the slide. He describes the display-flight as silent, whereas in Trinidad, although the flight is unaccompanied by mechanical sounds, the characteristic calls associated with it make it far from silent. He says that wing-flicking on the perch is sometimes accompanied by a snapping sound, which I never heard. Finally, he describes how the white patch on the under-side of the wing is exhibited in display, by a posture to which there is no parallel in the Trinidad bird.



TEXT-FIG. 2. The upright posture. (Drawn from movie film).

Further observations may show that not all these differences are real ones; even so, it seems clear that we have in this species an outstanding example of subspecific differences in display which would repay detailed study. It would be desirable to have a motion picture record of the displays of the Brazilian birds for comparison with the Trinidad population.

RELATIONSHIPS BETWEEN MALES

As in *Manacus* (p. 79), neighboring males usually show little overt aggressiveness towards each other, but they are in fact potentially aggressive. Hostility increases when a female visits the display ground, and it was on such occasions that the few flight chases between adult males were seen. Each male defends its perch against

intruders mainly by means of displays (especially landing beside the intruder in the upright posture, backward-slides, and wing-raising), but fights were never observed, as they were several times in *Manacus*, nor was there any evidence of one male trying to usurp another's display perch. Presumably Golden-headed Manakins can find new display perches more easily than Black and White Manakins can clear new courts, so that serious competition for display perches will be rare.

Neighboring males spend much time sitting quietly side by side on some perch usually between their two display perches. The most striking feature of this behavior is that both birds constantly face away from each other. Sometimes one bird shows its aggressiveness by an occasional backward-slide towards the other, or by suddenly raising its wings and fanning its tail (as at the end of the full backward-slide), and in such cases it may be seen that of the two birds the subordinate one has its head more completely averted than the displaying bird.

As in *Manacus* (p. 80), which has similar behavior, birds sitting with a neighbor spend more time at the display ground than those that are alone. This is especially noticeable when display is slack. Frequently they leave the display ground together and return together, which suggests that they associate together even when feeding. During an all-day watch on April 29, 1961 (p. 190), the male that was being watched continuously (Male A) sat with his nearest neighbor (Male B, whose display perch was only a few feet away in the same tree) for a total of 3 hours 44 minutes, in 48 spells, most of which were from 2 to 6 minutes long. Usually they sat together between their display perches, but sometimes on another perch several yards away in another tree. Male A also several times sat with another male several yards away, and Male B sat with two other males.

More than two males never sit together at the same time. This is a matter of common observation, but it was once seen especially clearly, when Male B was sitting with another male on a perch where he sometimes sat with Male A. Male A was sitting on a lower perch by himself about 30 feet away. The male with B flew off, and Male A, who appeared to have been waiting for this to happen, at once flew up and sat by Male B.

During the moult, when some males are absent, those that remain visit the unoccupied display perches and keep less strictly to their own, exactly as was found in *Manacus* (p. 79). Thus although there seem to be numerous suitable

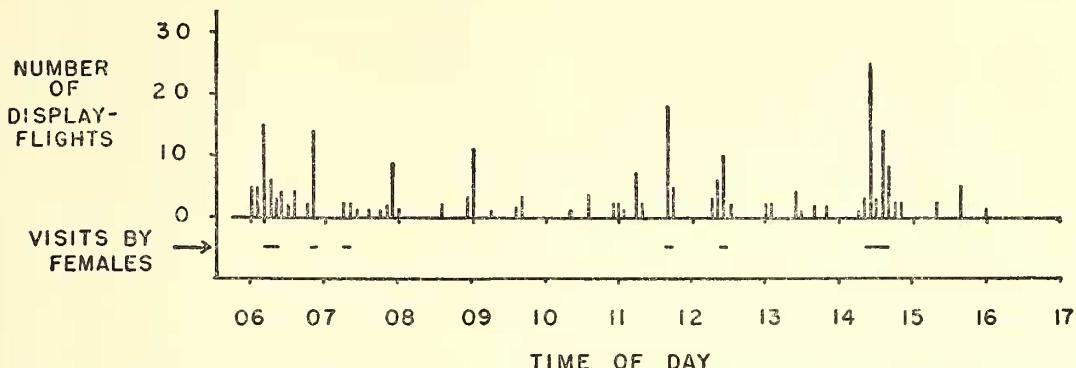
display perches in the area of the display ground, those that are actually "owned" by a male have a special significance for other males. It seems most likely that it is the mere fact that they have been occupied by another male that gives them this significance, rather than that they are especially suitable in some way not apparent to the human observer.

At the display ground that was under regular observation for a year, the display perches of six males were in view from the hide. Of the males that eventually occupied them after the moult, one was unbanded, one was banded with a numbered and a colored ring, and four were banded with numbered rings only and so were not individually distinguishable in the field. (The main trapping area, where over 600 individuals were caught, was about 200 yards away from this display ground.) Except for the unlikely possibility that the similarly banded males changed places with each other without any disturbance in their behavior being noted, these individuals kept to the same display perches throughout the greater part of the period of observation. The only observed changes took place as the time of moult approached; in June the color-banded male moved and displaced one of the banded males from a neighboring display perch, without however completely abandoning his former perch. The displaced male was not seen again, and may in fact have begun to moult (the earliest birds begin in July, Text-fig. 6). In July two more males disappeared and presumably began to moult. The color-banded male began to display occasionally at the perch of one of them, so that he now displayed at three perches. The display perch of the other male that had disappeared (Male A) was occupied by Male B, his close neighbor. The three males that remained were present throughout August, but in early September they all disappeared.

Text-figure 5 shows that a little display was recorded in September at this display ground. It was due entirely to a few newly arrived birds, probably recently moulted young males (p. 194). They did not use the display perches of the old males, but displayed on various perches round the periphery of the display ground.

Behavior of Juvenile Males

On many occasions groups of two or three birds in female plumage were seen away from display grounds performing uncoordinated display in a similar way to that described for juvenile male *Manacus* (p. 80). By analogy with *Manacus* they were assumed to be juvenile males, but this was not proved. Occasionally they were accompanied by adult males. All the



TEXT-FIG. 3. Diurnal rhythm of display, April 29, 1961. Intensity of display measured by number of display-flights in each 5-minute period (vertical lines).

display movements were made, but the display-flight was not usually followed by the backward-slide; displays tended to be incomplete and uncoordinated. In these groups presumed young male Golden-headed Manakins were occasionally seen associating with female-plumaged Black and White Manakins, and on one occasion a Black and White Manakin known from its later history to have been a juvenile male was seen displaying quite persistently to a Golden-headed Manakin. Parkes (1961) has discussed these observations in relation to the occurrence of occasional hybrids in the Pipridae.

COURTSHIP AND COPULATION

I was usually unable to be certain of the sex of the female-plumaged birds that I saw visiting the display grounds. The behavior of these birds seemed usually to be more ambivalent than that of the female-plumaged *Manacus* (p. 77), which were normally easy to sex after they had been watched for a little in the field. Eye-color sometimes provided a clue (p. 196), but was not usually observable accurately enough from a distance of several yards. Few color-banded birds were seen visiting the display grounds. Information on the behavior of males towards females is thus far less satisfactory than for *Manacus*.

I was unable to find many distinctions between displays given to birds presumed to be females not ready for copulation and those given to birds presumed to be juvenile males. In both cases the owning male and the visiting bird are both aggressive, and the situation is usually confused. The owning male will land beside the visitor in the upright posture, and may then slide backwards towards it. The other may fly away and return, also landing in the upright posture. Both birds may dart back and forth, perform

about-faces, flick the wings, or turn away from the other and raise the wings and fan the tail.

But when the visitor was a (presumed) receptive female, there tended to be a more orderly sequence of display. Typically the males would start by repeated darting back and forth, uttering the thin "zit, zit," and would then change to display-flights. If the female went to a male's display perch, he would continue his display-flights, landing close beside her, interspersing them with the upright posture, backward-slides, and other elements of his display.

Copulation was seen only twice, and attempted copulation once. On April 26 a female came to the display perch of the male that was under observation and perched there in normal posture. He flew away and came back in display-flight, landing immediately beside her. She remained still and he mounted. A little later the female returned to the same perch. The male flew in again in display-flight and landed beside her, but she then flew away. On April 29, during the all-day watch, a banded female flew to Male A's perch. He flew towards her from about two feet away, landed beside her in the upright posture, and mounted. On August 29 Male B, in the course of confused mutual displays of the sort described earlier in this section, attempted to mount a female-plumaged bird that was very aggressive and was thought to be a juvenile male. On this occasion mounting was not preceded by a display-flight.

Very many times males were seen to fly in with display-flight and land close beside a female, or presumed female, that had come to their display perches. Normally the female at once flew away to another perch. Flights to the female from a short distance, followed by the upright posture, were less often seen. Probably therefore the copulation sequence seen on April 26 is the most usual.

In *Pipra mentalis*, Skutch (1949) has described how the male lands straight on the back of the female after performing a circling flight. Although it is not easy to be sure of the details of the male Golden-headed Manakin's extremely rapid display movements, I had no evidence that they attempted to land straight on the female in this way.

THE DAILY CYCLE OF DISPLAY

An all-day watch was carried out on April 29, 1961, at the display ground that was under regular observation. All display-flights were counted from dawn to the time that display ended. From Text-fig. 3, which gives the results of this watch, it will be seen that after an early-morning outburst of display, activity fluctuated rather irregularly until 1545, when display ceased for the day. There was an especially intense bout of display between 1400 and 1500. The early-morning watches that were carried out weekly for over a year at this display ground showed that the time when the early outburst of display occurred was not constant. On some mornings there was little display between 0600 and 0700, and the main outburst was between 0700 and 0800. Later in the day, too, the times when display was most active were variable. In this respect the Golden-headed Manakin shows a less well-marked daily rhythm than *Manacus* (p. 75).

Text-fig. 3 also shows the times when females, or presumed females, visited the display ground. As would be expected, the presence of a female coincided with outbursts of display. Because of the difficulty of seeing the cryptically colored females unless they move, it was not easy to tell whether it was the arrival of a female that stimulated the males to display, or an outburst of display that attracted the females. It seems, however, that it is usually the arrival of a female that stimulates the males. Nevertheless outbursts of display certainly occur without any females being present, because, as in *Manacus*, the males at a display ground have a mutually stimulating effect on one another, so that when one starts to display others often follow and a general outburst results.

During the all-day watch, a record was kept of the periods of presence and absence of a male that had a display perch near the hide (Male A, mentioned above). This bird had occupied the same perch for at least 8 months; his habits and alternative perches were well known. His three nearest neighbors were all banded, but he was not. Between 0548, when he arrived, and 1700, when he was still present but display had long since ceased and the light was too bad for further

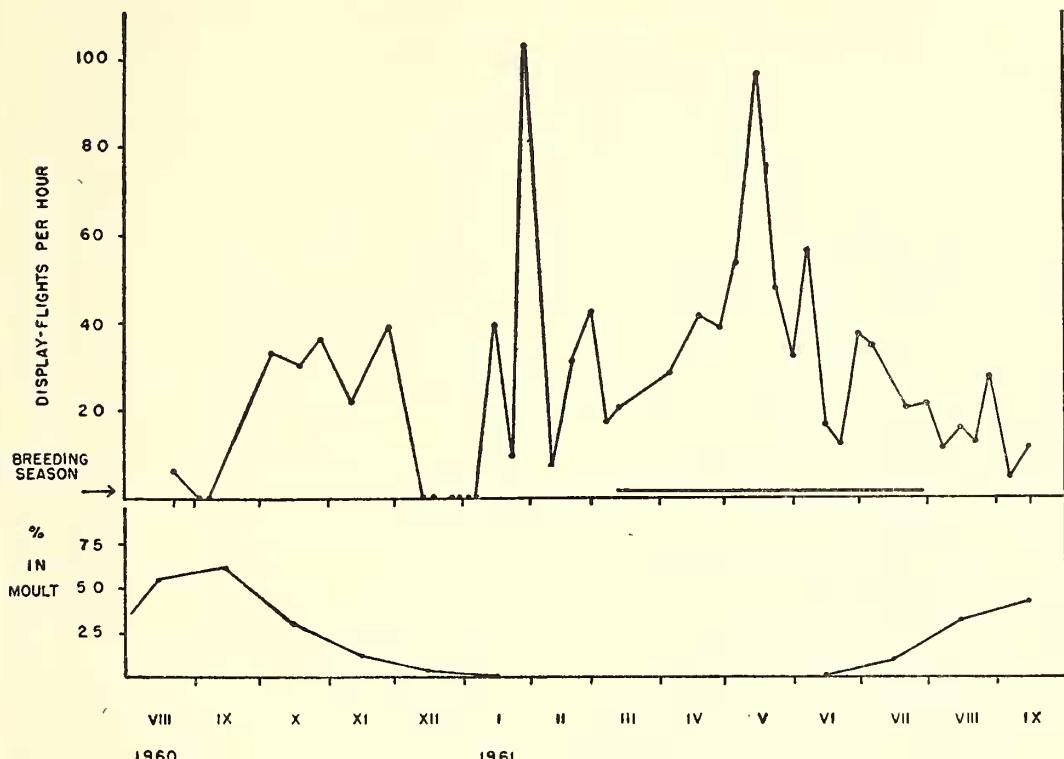
observation, he was present on or near his display perch for 88% of the time. His 43 absences were mostly very short, 29 of them being from $\frac{1}{2}$ to $1\frac{1}{2}$ minutes. It is probable that some of them were due to his merely flying for a short time to a perch that was out of sight. During one of the longer absences, of 5 minutes from 1612 to 1617, he bathed, as he returned with wet plumage and preened on a perch near his display perch. Excluding this absence, the time when he was away and could have been feeding was only 11% of the daylight hours.

An attempt was made to watch another male at the same time (Male B). His absences were of the same sort of length as Male A's, and they were often synchronized, as they occupied neighboring display perches, but it was not possible to obtain a complete record for this bird for the whole day. Less prolonged watching on many occasions gave no reason for supposing that the behavior of the males under observation on this day was in any way unusual.

THE ANNUAL CYCLE OF DISPLAY

Male Golden-headed Manakins display at all times of the year, except when they are moulting, but the intensity of display fluctuates somewhat throughout the season. During the regular early-morning watches at the main display ground under observation from August, 1960, to September, 1961, the intensity of display was measured by counting all the display-flights, a procedure which is rather easy as the display-flight is accompanied by a quite characteristic series of calls (p. 186). Text-figure 4 shows the intensity of display throughout a year, as measured during these watches. This figure also shows the season of moult in the two years 1960 and 1961, and the breeding season as far as it was ascertained, and thus provides a conspectus of the annual cycle for just over a complete year. It will be seen that display stopped during the moult in 1960, but not in 1961, when it was merely reduced. As mentioned above, the display in September, 1961, was not from the old established males, who had all begun to moult by then, but from newly arrived, probably recently moulted young males.

A more marked break in display occurred in December, 1960, and January, 1961, at exactly the same time as a break occurred in the display of *Manacus* (p. 82). Though there was evidence that food was temporarily short in the Arima Valley, where the observations were made, Golden-headed Manakins ceased displaying equally completely for the same period in an area of forest several miles away on the north side of the Northern Range, where food was



TEXT-FIG. 4. Annual cycle of display, breeding and moult, August, 1960, to September, 1961. Upper graph: intensity of display during early morning watches, based on number of display-flights per hour, and breeding season (horizontal line). Lower graph: moulting seasons, showing percentage of trapped adults undergoing wing-moult in each month.

abundant. The reason for the cessation of display was therefore not clear. Regular observations were not made all through December and January in other years, so breaks in display during that period could have gone undetected, but regular observations at a display ground of *Manacus* showed no comparable break in display in other years.

BREEDING

The Golden-headed Manakin's nest is typical of the family, a small, shallow cup slung in the fork between two horizontal twigs of a sapling or shrub, or the lower branches of a tree. It is thinly woven of brownish fibers and rootlets, and often has a few dead leaves bound into the bottom of the cup or hanging from the underside. The cup is usually so thin that the contents are partly visible from below. Those that were seen lacked the lining, made of the branching panicles of the melastomaceous herb *Nepsera aquatica*, that was found to be so characteristic of the nest of *Manacus* (p. 89).

Eight of the 15 nests that were found were between 4 and 8 feet above the ground. The other seven were from 10 to 35 feet. Probably

a much higher proportion of the nests are high up than these figures indicate, since high nests are much less easy to find. Since the low nests are not much less easy to see than the nests of *Manacus*, there seems no other way to account for the fact that only 15 were found compared with over 300 of *Manacus*, although the Golden-headed Manakin is the more abundant of the two species.

For 11 of the 15 nests, which contained eggs or young, the months of laying were as follows: March, 1; June, 4; July, 5; August, 1. The months of laying of the two nests recorded by Belcher & Smooker (1937) were January, and late March or early April. Four nests were found while being built, and so far as known no eggs were laid in them or, if laid, they were lost soon after; all these were in April and May. In addition, birds with incubation patches were trapped in May and July, and an egg-laying bird in March. It seems then that the breeding season extends from January to August, and that most clutches are laid in the latter half of this period—a breeding season substantially the same as that of *Manacus* (p. 82).

Few details of breeding were obtained, due to the high rate of nest failure. Four of the completed clutches consisted of two eggs, and one of one egg. The interval between the laying of the eggs was ascertained at two nests to be two days. One egg was found to have been laid between 1145 and 1545 hours. At one nest the incubation period was found to be 16 or 17 days. The fledging period was not ascertained, since none of the seven nests found before the time of hatching survived to the time of fledging.

FEEDING HABITS

Golden-headed Manakins feed in much the same way as Black and White Manakins; they pluck fruit on the wing, swallowing it whole on landing, and pick insects and spiders in flight from the twigs and foliage. The most obvious difference between the two species is that on average Golden-headed Manakins feed higher above the ground. Another probable difference is that they take relatively more insect food. Thus male Golden-headed Manakins at their display grounds regularly dart off for short sallies and pick food from the underside of leaves and from twigs, but Black and White Manakin males were never seen to do this. Probably there is more suitable insect food in the trees at the level at which Golden-headed Manakins display than near the ground where the Black and White Manakins have their courts, and probably also Golden-headed Manakins are the more fitted of the two species for this method of feeding, as they are far more agile on the wing.

Stomach contents of several birds were examined, but as most of them were trapped near places where fruit was abundant they yielded

no valid information on this point. The stomach of a bird accidentally killed away from a trapping place contained remains of a spider 13 mm. long, a small beetle, a dipteran, an unidentified winged insect, an insect larva, and a few seeds and the skin of the berry of a melastomaceous tree.

Golden-headed Manakins are a little smaller than Black and White Manakins, and it seems that they cannot take such large fruits. Of the three largest fruits found to be eaten by *Manacus* (p. 92), 15-19 mm. long and 10-16 mm. in diameter, Golden-headed Manakins were seen to take only one (*Protium heptaphyllum*, 15 by 11 mm.).

Altogether, 445 records were obtained of Golden-headed Manakins feeding on the fruits of 43 species of plants (Table I). All but two of the plants were identified, at least down to generic level. All the fruits taken were small berries which were swallowed whole, with one exception: a bird was once seen picking pieces in flight from the large fruit of a species of *Henriettea* (Melastomaceae).

As for *Manacus* (p. 93), the Melastomaceae was found to be by far the most important family of food plants: 11 species were seen to be fed on, accounting for 63% of all the records. In number of species the Rubiaceae, with 6 species, came next, but very few records were obtained for each, and their total was only 2% of the whole. For *Manacus*, 14% of all records were from Rubiaceae. The difference is probably due in part to the higher level at which Golden-headed Manakins feed; the Rubiaceae with small fruit, likely to be most attractive to Golden-headed Manakins, (especially *Palicourea*, *Cephaelis*, *Gonzalagunia* and *Psychotria*),

TABLE I. FRUITS EATEN BY GOLDEN-HEADED MANAKINS IN THE DIFFERENT MONTHS

Species	Numbers of records in different months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
MORACEAE												
<i>Ficus citrifolia</i>			1									
<i>Ficus clusiifolia</i>	4	5	3	5	1					3	7	
URTICACEAE												
<i>Trema micrantha</i>						2						
NYCTAGINACEAE												
<i>Pisonia eggersiana</i>									3			
LAURACEAE												
<i>Ocotea canaliculata</i>	6		1									
<i>Phoebe elongata</i>		2		1								
BURSERACEAE												
<i>Protium heptaphyllum</i>									3			

TABLE I. FRUITS EATEN BY GOLDEN-HEADED MANAKINS IN THE DIFFERENT MONTHS (*continued*)

Species	Numbers of records in different months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
EUPHORBIACEAE												
<i>Alchornea triplinervia</i>				4								11
<i>Hieronyma caribaea</i>			2								2	
<i>Maprounea guianensis</i>												5
<i>Sapium aucuparium</i>								4				
AQUIFELIACEAE												
<i>Ilex</i> sp.												1
TILIACEAE												
<i>Sloanea laurifolia</i>		5										
<i>Sloanea stipitata</i>				3								
DILLENIACEAE												
<i>Davilla aspera</i>				1								
<i>Doliocarpus dentatus</i>					5	4						
<i>Pinzona calineoides</i>			1									
FLACOURTIACEAE												
<i>Laetia procera</i>		5				1						2
MYRTACEAE												
<i>Myrcia leptoclada</i>		2										
MELASTOMACEAE												
<i>Henriettea</i> sp.												1
<i>Miconia affinis</i>												
<i>Miconia chrysophylla</i>					6	10	7	12	1			
<i>Miconia guianensis</i>	18	8	1	4								
<i>Miconia kappleri</i>	4											
<i>Miconia multispicata</i>		2	10	7	3							
<i>Miconia myriantha</i>				1								
<i>Miconia prasina</i>					1	20	4	25	11			
<i>Miconia punctata</i>	3											4
<i>Miconia splendens</i>					2							
<i>Miconia tomentosa</i>						2	4					
<i>Miconia</i> sp.										3	6	
ARALIACEAE												
<i>Didymopanax morototoni</i>										13	32	
VERBENACEAE												
<i>Aegiphila integrifolia</i>												5
PHYTOLACCACEAE												
<i>Phytolacca icosandra</i>						1						
SOLANACEAE												
<i>Cestrum baenitzii</i>							2					
RUBIACEAE												
<i>Cephaelis muscosa</i>							1					
<i>Isertia parviflora</i>												1
<i>Malanea macrophylla</i>				1								
<i>Palicourea crocea</i>												
<i>Psychotria inundata</i>											3	
<i>Psychotria marginata</i>												1
COMPOSITAE												
<i>Wulffia baccata</i>								1				
Unidentified vine (1)							1					
Unidentified vine (2)												2
Number of species	4	5	6	9	12	7	5	5	3	6	9	8

are shrubs or low trees, while the larger rubiaceous trees and vines which are at the level where Golden-headed Manakins mainly feed (*Amaioua*, *Coussarea*, *Lacistema*, *Malanea*) have larger fruits which are at or near the upper limit of size for Golden-headed Manakins.

Of the other families, the Euphorbiaceae, Moraceae and Araliaceae were the most important. Four species of Euphorbiaceae contributed 6% or all the records, and two species of *Ficus* (Moraceae) 5%. Apart from some of the melastomes, the greatest number of records from a single tree species came from *Didymopanax morototoni* (Araliaceae), which contributed 10% of the total.

The number of fruit species found to be eaten in each month varied from 3 in September to 12 in May. Most different kinds of fruit were found to be eaten in the months April-June and November-December. Though the species involved are partly different and the total numbers smaller, this is the same picture as was found for *Manacus* (p. 93) and suggests that the availa-

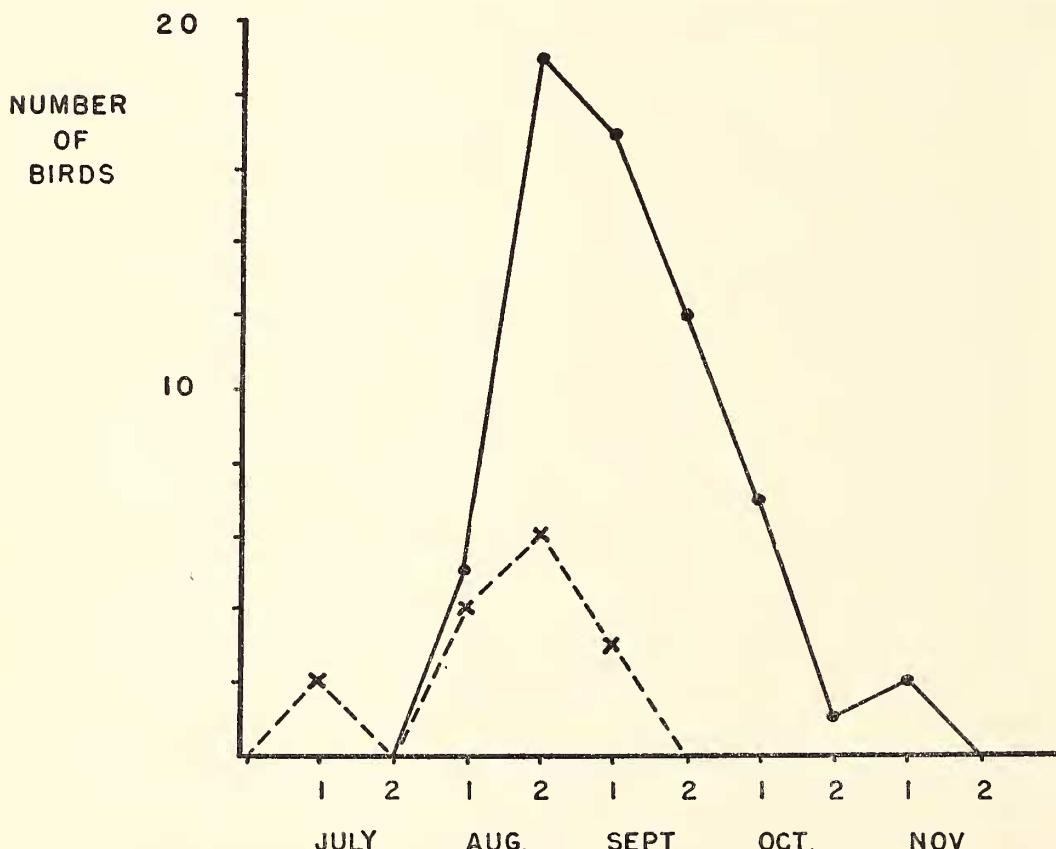
bility of fruit shows a double peak in the year, of which the first, major peak comes in the middle of the breeding season.

PLUMAGES, MOULTS AND COLOR OF SOFT PARTS *Moults*

The moults follow the same course as in *Manacus* (p. 82). There is a slow post-juvenile moult in the first year of life, involving the head and body, lesser wing-coverts and some inner secondary major coverts. Most of the birds undergoing this post-juvenile moult were trapped in the months August-January. The next moult, to adult plumage, is complete and takes place in the second summer and autumn. Thereafter there is an annual moult in the months August-November.

Fifteen birds were trapped while moulting from juvenile to adult male plumage. As was found in *Manacus* (p. 85), these birds on average moulted earlier than the adult males (Text-fig. 5).

Four birds were trapped twice in the course



TEXT-FIG. 5. Moult seasons of old and young males. Solid line: fully adult males trapped in moult. Broken line: males trapped while moulting from juvenile to adult plumage.

of a single moult. The amount that the moult of the wing-feathers had progressed between the two captures showed that the complete moult must last about 90 days, a figure similar to that obtained for *Manacus* (p. 85). Four birds trapped while moulting in two or three different years showed slight annual variations in the timing of their moult. In the population as a whole, the season of moult did not vary much in the four years for which data were obtained (Text-fig. 6), except that it ended earlier in 1958 than in 1959 and 1960.

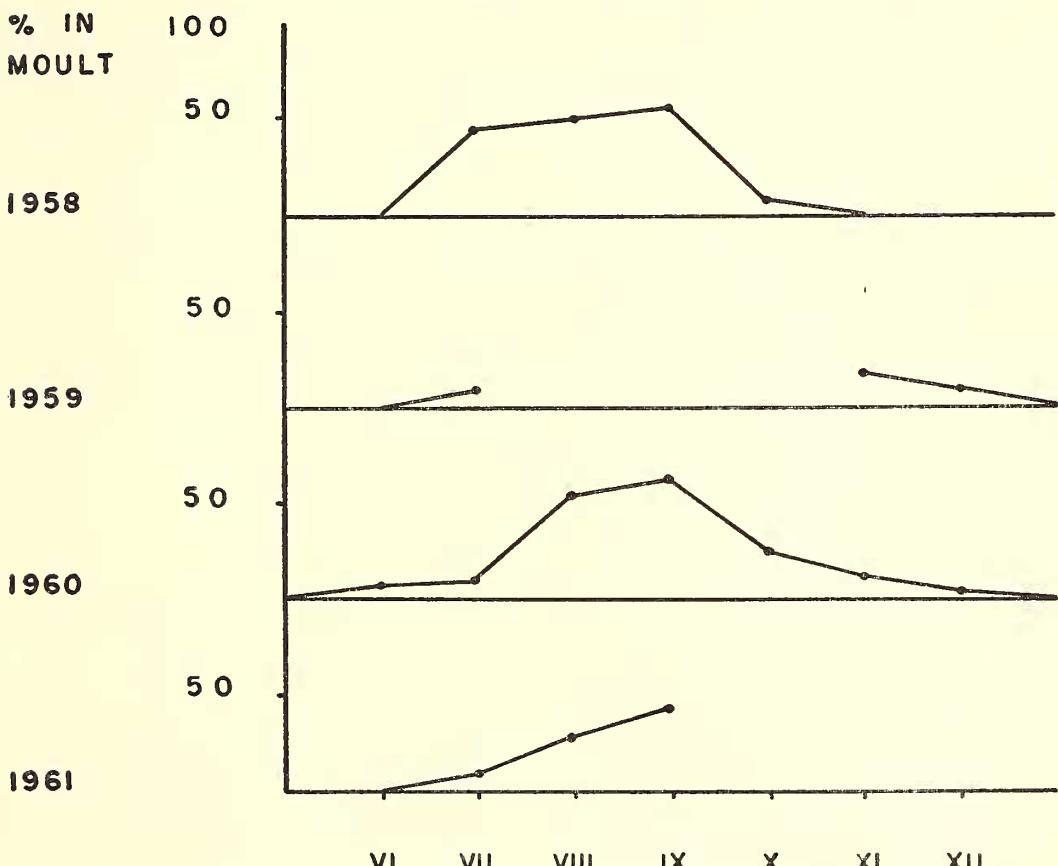
Plumages

Female Golden-headed Manakins regularly have a few male-type feathers in the head and body plumage, and in those that were trapped more than once the number and distribution of these feathers remained much the same from one year to the next. Juvenile males also often have a few adult male feathers in the head and body, so that on the basis of plumage they can-

not be separated from adult females. A small proportion of the adult males had some female-type feathers in the plumage. Usually only a few were scattered here and there, but two adult males had the plumage of the underparts almost entirely female, and many female-type feathers elsewhere in the plumage; and one had all the feathers of the head and body of partly male and partly female color. A fourth had a completely mixed plumage, with male and female-type feathers intermingled in the head, body and wing. This bird was trapped four times over a period of just over two years, and its plumage remained exactly the same.

Five birds in female plumage and one adult male had partially albino plumage. In all of them, the dark pigment was lacking in some of the flight-feathers, which were white or pale yellow.

In addition to these variations, the general body color of birds in female plumage varied



TEXT-FIG. 6. Moult seasons, 1958-1961. Each graph shows the percentage of trapped adults undergoing wing-moult in each month, based on the following totals: 1958, 122; 1959, 104; 1960, 254; 1961, 124. Gaps in 1959 and 1961 indicate periods when no observations were made. (A single bird moulting in March, 1961, is not shown).

considerably, from the usual olive-green to a paler, yellower green. Several birds had a pale crown-patch of the same shape as the adult male's golden cap.

Variation in plumage is much greater in the Golden-headed Manakin than in *Manacus*, in which only three slight abnormalities of plumage were found in the 275 individuals caught in the study area. The reason for the difference is quite obscure, but it may be noted that it applies also to the color of the iris, beak and legs, as described in the following sections.

Eye-color

The iris of adult males is white. Only one exception was found to this rule: the male with mixed plumage, mentioned above, had its iris mainly white but bordered with gray-brown around the pupil. In birds of female plumage the iris is variable, ranging from gray-brown or seal-brown (as in juveniles) to white through various intermediates in which it is blotched, dotted, mottled or clouded with varying amounts of white.

It has previously been assumed (e.g., Conway, 1959) that birds in female plumage with some white in the eye are juvenile males. However, analysis of the eye-color of the birds that were trapped more than once showed that the situation is far from simple, and in particular, that birds with intermediate eye-colors are more often females than juvenile males.

Twenty-seven known females were retrapped after an interval of 8 months or more. In 19 of them, the iris was dark when they were first trapped. In 13 of these, the iris remained dark after intervals of 8 months to 2½ years; in the other 6, the iris was spotted or flecked with white when they were next trapped, after intervals of 8 months, 1 year, 1 year, 2 years, 3 years and 3 years. Eight known females had varying amounts of white in the iris when they were first trapped. In four of them the eye appeared unchanged when they were next trapped, after intervals of 9 months to 1 year 8 months; in two the white spots had enlarged, 1 year 8 months and 2 years later; and in two the white spots later disappeared. One of these two, trapped four times, had small white spots which remained for a year, then disappeared four months later. The other, trapped three times, had large white spots when first trapped; five months later it had small spots, eight months after that the eye was dark, and 2 years and 4 months after that it again had a partially white iris. On this last occasion it also had 2 white flight-feathers in one wing and one white feather in the other wing; previously its plumage had been normal.

There must be a greater tendency for white spots to appear and increase in the course of a female's life than to decrease, as they all start life with dark eyes; but the amount of white does not usually increase indefinitely. This is shown not only by the evidence given above, but also by the fact that no bird that was definitely known to be female had an all-white eye. Twenty birds were trapped in female plumage, with an all-white eye. Three of them were later found to be males, and eight others probably were, as they were trapped at the season when the eye-color of juvenile males changes to white (May-July). Thus not more than 17, and probably less than half that number, of the approximately 300 females that were trapped could have had white eyes.

Nine males were trapped in juvenile plumage and then retrapped after moulting to adult male plumage. Four of them, first trapped in their first November, December and January (2), all had dark eyes (as had two juvenile males collected in October). Of the other five, one was trapped in the April before its moult and had a light gray, slightly mottled iris; one in May had the iris gray, clouded with white; and three in June all had the iris white, one of them being still rather dull. In addition to these birds that were trapped before and after their moult to adult plumage, fifteen young males were caught while moulting to adult plumage. In 13 of them the eye was fully white, and in the other two it was white, faintly clouded with gray.

Thus the eye-color of these males changed to white in the last few weeks before they moulted, the intermediate stages being uniform gray, or clouded or faintly mottled with white. None had the iris dark with white spots, as in females.

Color of Beak and Legs

The upper mandible is straw-yellow in adult males and horn-brown in females and young birds; the lower mandible is yellowish in all birds, paler in males than females. Within the sexes there is some individual variation, and in adult males seasonal variation too was found, the color of the upper mandible becoming darker at the time of the moult.

The color of the legs varies, from the usual flesh-pink to dull grayish pink and even occasionally blue-gray. It seemed probable that the birds with the darkest, grayest legs were mainly young birds, but this was not proved.

SUMMARY

The Golden-headed Manakin, *Pipra erythrocephala*, was studied in an area of primary and secondary forest in the Northern Range of

Trinidad. On the study area it was the most abundant forest bird, with an adult density in excess of one bird per acre. The annual mortality of adults was estimated to be about 10%.

The males display at communal display grounds, where each occupies a display perch 20-40 feet up in a tree. Display grounds persist year after year in the same places.

The various display movements are described and figured. The most conspicuous display consists of a rapid swooping flight to the perch, followed by a backward-slide, with associated wing and tail movements. Copulation follows immediately after a display-flight.

Neighboring males are potentially hostile to each other, but little overt aggressiveness is shown. Pairs of males spend much time sitting side by side mid-way between their display perches.

The males spend about 90% of the daylight hours at their display grounds, and are normally present at them all through the year except when they are moulting.

The breeding season extends from January to August. The nest, a thinly woven cup slung in the fork between two horizontal twigs, is placed from 4 to 35 or more feet above the ground. None of the nests found survived to fledging.

The food consists of berries and small invertebrates, taken on the wing. Observations showed seasonal variations in the amount of fruit available, with peaks in April-June and November-December.

Moults and plumages are described. There is a slow post-juvenile moult in the first year, followed by a complete moult in June-September. Subsequent annual moults occur a little later, in July-November.

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APPENDIX

WEIGHTS AND MEASUREMENTS

As for *Manacus* (p. 102), birds were placed in a cloth bag and weighed immediately after being trapped. A spring balance accurate to 0.5 gm. was used.

Weights have been used only for birds of known sex. A very large number of weights of birds in female plumage, which were never retrapped and so could not be sexed, have been discarded.

Similarly wing-lengths are given only for birds of known sex.

Wing-lengths

Wing-length (mm.)	Adult males	Juvenile males	Females
62			1
61			4
60	2	5	15
59	13	4	28
58	42	7	14
57	79		4
56	64	1	1
55	30		
54	5		1
53	1		
52	1		
Totals	237	17	68
Means	56.7	58.7	58.9

Weights of Adult Males

Weight (gm.)	Months						All months
	I-II	III-IV	V-VI	VII-VIII	IX-X	XI-XII	
17	1						1
16							1
15				3	3	2	8
14.5		2		2	4		8
14	1	1	1	5	11	6	25
13.5	4	3	3	11	12	8	41
13	4	5	16	11	13	7	56
12.5	15	10	9	10	9	11	64
12	10	6	11	7	8	9	51
11.5	5	4	6	5	2	7	29
11	2		2			2	6
10.5					1		1
Totals	42	31	48	54	63	53	291
Means	12.5	12.6	12.5	13.0	13.2	12.8	12.79

Weights of Juvenile Males

Weight (gm.)	All months
13.5	2
13	2
12.5	3
12	2
Total	9
Mean	12.7

Weights of Females

Weight (gm.)	Months						All months
	I-II	III-IV	V-VI	VII-VIII	IX-X	XI-XII	
16.5		1					1
16			3	5		3	11
15.5		1	3	8	2	1	15
15		1	5	13	5	5	29
14.5	3	5	3	11	13	3	38
14	9		5	4	16	10	44
13.5	9	3	3	5	9	5	34
13	6	1	3	5	6	5	26
12.5	2	1	2	1	2	4	12
12	1			1	2		4
Totals	30	13	27	53	55	36	214
Means	13.5	14.3	14.4	14.6	13.9	14.0	14.12